



Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at <http://about.jstor.org/participate-jstor/individuals/early-journal-content>.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.

BOTANICAL GAZETTE

SEPTEMBER, 1901

GAMETOGENESIS AND FERTILIZATION IN ALBUGO.
CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY.
XXIX.

FRANK LINCOLN STEVENS.

(WITH PLATES I-IV)

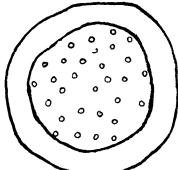
[Continued from p. 98.]

II. PHYLOGENETIC.

THIS study of *Albugo* has established a series of forms showing advances in certain respects and a marked reduction in others. The species are closely related, and the difference between two consecutive members of the series is not great, although the extremes are widely divergent. There are four prominent structures or conditions connected with the series, namely, the coenocentrum, the receptive papilla, the mode of zonation, and the number of functional nuclei. Arranged in the order of these characters the species may be listed as *A. Portulacae*, *A. Bliti*, *A. Tragopogonis*, and *A. candida*. In this series the coenocentrum constantly increases in complexity of structure and perfection of function, the receptive papilla becomes less conspicuous, the number of functional nuclei decreases, and the mode of zonation varies in the last two species. These conditions are graphically represented in the accompanying figure which is self explanatory. We may consider the series as a possible expression of the phylogeny of the genus. Which conditions are likely to be primitive?

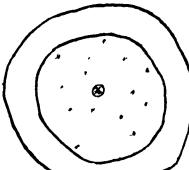
The coenocentrum increases as the receptive papilla decreases; either one or the other must be retrograding. From a study of these two structures alone it might be difficult to determine the true history, but a consideration of the manner in which the

A. Bliti and *A. Portulacae*.



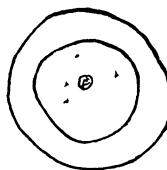
Many functional.

A. Tragopogonis.



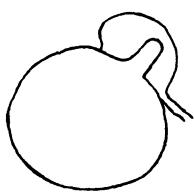
Many potential and functional.

A. candida.



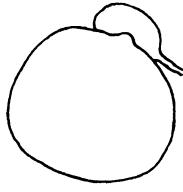
NUMBER OF FUNCTIONAL NUCLEI DIMINISHING

A. Bliti and *A. Portulacae*.



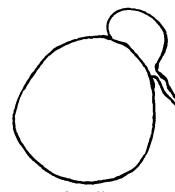
Large.

A. Tragopogonis.



Small.

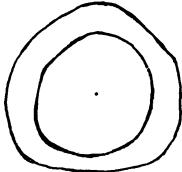
A. candida.



Smaller.

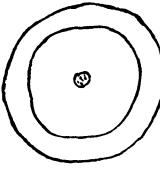
RECEPTIVE PAPILLA DIMINISHING.

A. Bliti and *A. Portulacae*.



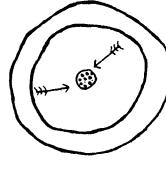
Small.

A. Tragopogonis.



Large, nutritive.

A. candida.



Larger, nutritive and strongly chemotactic.

COENOCENTRUM ADVANCING IN STRUCTURE AND FUNCTION.

oosphere of *A. Tragopogonis* attains the uninucleate condition shows that this structure in its ontogeny passes through a stage identical with that reached by *A. Portulacae* and *A. Bliti* in their full maturity, thus giving an excellent illustration of the biogenetic law. Both the antheridia and oospheres of *A. Tragopogonis* are multinucleate in their earlier stages, and the development is

strictly comparable to that of *A. Portulacae* and *A. Bliti*, stage for stage. Later the supernumerary oospheric nuclei are eliminated, leaving only one female pronucleus to function. It seems necessary, therefore, to regard the supernumerary oospheric nuclei in this species as potential gameto-nuclei, and to regard the uninucleate condition in *A. Tragopogonis* as due to the suppression of the many and the survival of only one gameto-nucleus. In the light of this behavior *A. Portulacae* must be regarded as the primitive form, and *A. candida* the most highly developed. In view of the great functional importance of the coenocentrum in *A. candida* and *A. Tragopogonis*, it is also rational to regard the coenocentrum as an advancing structure. The reverse is true, however, in reference to the receptive papilla, as there is no indication of its present utility, and everything indicates that it is a vestigial structure. The difference in the mode of zonation between *A. Tragopogonis*, where the protoplasm aggregates into preliminary centers which finally coalesce into one, and *A. candida*, where one central region is formed directly by a recession of the protoplasm from the oogonial wall, may well be regarded as an outcome of the reduction of *A. candida* to a uninucleate condition of the oosphere, and may be taken as further evidence indicative of the highly developed rather than the primitive condition of *A. candida*. It is hardly conceivable that evolution could have proceeded in the reverse direction, that is from the type of oogenesis in *A. candida* to that of *A. Tragopogonis*, *A. Bliti*, and *A. Portulacae*. The serial evidence from the coenocentrum, the receptive papilla, the mode of zonation, and the number of functional nuclei concurs in pointing to the multinucleate conditions shown in *A. Portulacae* and *A. Bliti* as primitive, and the uninucleate oosphere of *A. candida* as derived.

The conditions are almost precisely the same as those in the Fucaceae studied by Oltmanns (1889), with the exception that in Albuginaceae and Peronosporaceae a coenocentrum plays an important rôle in the reduction of the number of functional nuclei to its ultimate expression. It is not difficult to imagine

that the process of evolution of one form from another may have been very rapid after the development of the nutritive region, the coenocentrum. In *A. Portulacae* and *A. Bliti* the struggle between sister gameto-nuclei is possibly close, but the conditions are quite different in forms possessing a highly developed trophoplasmic area in the center of the oosphere, for it becomes a matter of much importance which nucleus is the first to reach and avail itself of the nutrition. The determining factors may be the position of the nucleus, its orientation, or its sensitiveness to chemotactic influences. In any event, a nucleus which gains more nutrition will contribute its substances to a larger fusion nucleus, and consequently leave stronger descendants to the next generation. Moreover, this action of natural selection, aside from furnishing stronger descendants, will foster exactly those characters which enabled the parent nucleus to prevail in the mother oosphere. In short, a condition obtains here which can easily be conceived as one that would conduce to a rapid evolution from a multinucleate to a uninucleate oosphere through the action of natural selection. It is a manifestation of what Klebahn (1899-1900) has termed "Streben nach Einkernigkeit der Sexualzellen," under such conditions that it is possible to recognize the cause of the "tendency."

A peculiarity, probably a consequence, of the uninucleate condition of the oospore of *A. Tragopogonis* and *A. candida* is the division of its fusion nucleus before the spore passes into the winter condition. A series of mitoses rapidly converts the spore from a uninucleate to a multinucleate structure. The division here, as in many of the higher plants, may be regarded as the initial step in germination. In the species with multinucleate oospores no mitoses occur until the long resting period, normally in this case the winter, is passed. In such forms, presumably the primitive ones, the intrasporal evidence of germination appears when the spore ruptures its coat and manifests externally the new activities. It is clear that the inception of division in one case is homologous with that in the other, and in both it constitutes the commencement

of germination. It matters not that in one instance it is before and in the other after the resting period. The divisions which in primitive multinucleate forms come after the resting period have in *A. candida* and *A. Tragopogonis* been transferred to a time before the winter rest. The condition is very similar to that presented in the spermatophytes, where intraseminal germination immediately following fertilization is the rule, although many orchids retain their one-celled condition indefinitely.

Although the division of the fusion nucleus is the first step in germination, the time of this mitosis is subject to variation in different types. The division is delayed in the forms of Albugo having multinucleate oospheres, in *Peronospora parasitica* (Wager 1900), in *Saprolegnia* and *Achlya* (Trow 1895 and 1899). The division occurs soon after fusion in species of Albugo having uninucleate oospheres, and in the Peronosporaceae (Berlese 1898). It appears from the consideration of these species that it is not simply a disproportion between the volume of the cytoplasm and the number of nuclei that induces division, for this disproportion is as great in the case of *Peronospora parasitica*, *Achlya*, and *Saprolegnia*, as in *A. Tragopogonis*. Wager (1900) has already indicated that in these species, in which the retardation of the fusion is most marked, the inception of division is also most delayed. He says (pp. 275-276):

Peronospora parasitica is at present the only member of the group with retarded nuclear fusion. . . . In this species it is delayed until the thick zygote membrane has been partly formed. The ripe oospore of *P. parasitica* is uninucleate. . . . In all the other species of Peronospora which have been examined the ripe zygote is multinucleate.

Similarly, Trow (1895, p. 648, and 1899, p. 175) finds that fusion is slow in *Achlya* and *Saprolegnia*, and likewise the division of the fusion nucleus does not occur until after the oospore has passed the resting period. This association of retardation in fusion with delay in division suggests that after the act of fusion is completed, so far as the microscope can give evidence, there may be further changes which the elements of the pronuclei must undergo before fusion is really completed.

The delay of division in species like *Saprolegnia*, *P. parasitica*, and *Spirogyra* (Chimelewsky 1888) may be due to a delay on the part of the nuclei in completely preparing for fusion, and to slowness in the act of fusion itself, an act which is not completed when the mere fusion made visible by our present powers of magnification is effected. In this connection Wager (1899, p. 578) makes this suggestion:

This difference in the behavior of the nucleus during the maturation of the oospore is probably connected with the mode of germination. DeBarry has already pointed out that in *Cystopus* and some other species the oospore on germination produces at once a mass of zoospores. In *Peronospora Valerianellae* and others the oospore at once develops a germ-tube. It may be, therefore, that the uninucleate condition of the zygote indicates germination by a germ-tube, and the multinucleate condition germination by the formation of zoospores.

Apart from the relationships within the group which stand out with more or less clearness, the cytological phenomena emphasize strongly the affinity between the Albuginaceae, Peronosporaceae, and Saprolegniaceae. *Peronospora parasitica*, according to the research of Wager (1900), has a uninucleate oosphere, which is fertilized by the entrance of one antheridial nucleus. In oogenesis the nuclei divide simultaneously while passing to the periphery, as in *Albugo*, and then one returns to the ooplasm. A highly developed coenocentrum is present, and exerts an attractive influence upon the nuclei even as they lie in the periplasm. All of these conditions, together with the presence of the receptive papilla, clearly attest a relationship between the Albuginaceae and Peronosporaceae. The highly developed coenocentrum and the presence of a uninucleate oosphere indicate that the Peronosporaceae are the more highly developed group. Their ancestors may have been some forms possessing a uninucleate oosphere, similar to that of *A. candida*, from which one of the mitoses has later been suppressed as superfluous. Merely from the evidence of oogenesis, the Peronosporaceae might be regarded as an offshoot from the Albuginaceae after the uninucleate condition had been attained; that is, they may represent a further development of the condition illustrated

in *A. candida*. But certain peculiarities of the asexual organs make such a view improbable. The Albuginaceae and Peronosporaceae may both have attained the uninucleate condition of oosphere independently, each being derived from ancestors having multinucleate oospheres. The probability of the multi-nucleate condition being the primitive one discredits the validity of Fischer's position (1892, pp. 223, 224) regarding the derivation of the Peronosporaceae and Saprolegniaceae from the Chytridiaceae.

Oogenesis in the Saprolegniaceae resembles that in the Albuginaceae in having a multiplication of nuclei through a mitosis, followed by a degeneration of the superfluous nuclei, thus presenting very closely the condition seen in *A. Tragopogonis*. Trow, Hartog, and Humphrey (1892) failed to report a coenocentrum, but Dangeard (1890) has described a structure in both Saprolegnia and Peronospora which may prove to be the same (*cf.* Wager 1896, pp. 308 and 322).

From my own studies, Pythium closely resembles Albugo in its oogenesis. There is a withdrawal of the protoplasm from the oogonial wall, differentiating a vacuolate periplasm, clearly homologous with that of Albugo. Cytological knowledge of the events of oogenesis in this genus will have great value in determining whether its relationship is closest to the Peronosporaceae or Albuginaceae. The present indications favor the Peronosporaceae, where it was placed by DeBary (1881).

Two diametrically opposed processes of oogenesis occur in the single-egged (eineiig) Albuginaceae and the many-egged (vieleiig) Saprolegniaceae. In the first there is a massing of protoplasm in the center, forming the rudimentary oosphere; in the second a peripheral accumulation of protoplasm leaves the central region comparatively free. There is in Peronospora, however, a movement toward the periphery rather than away from it, resembling in this respect Saprolegniaceae. It is conceivable that Pythium may represent a transitional condition between oogonia with single eggs and those with several, which

would accord with the theory of DeBary that the Saprolegniaceae evolved through the Peronosporaceae.

The origin of the Peronosporaceae and Saprolegniaceae from lower forms is far from clear. Before the discovery of the multinucleate oosphere in *A. Bliti*, a relation to some type like Vaucheria seemed probable. In Vaucheria many nuclei pass into the rudimentary oogonium, after which, as in *A. candida*, the superfluous nuclei retreat from the cytoplasmic region which is destined to become the oosphere. The essential difference is that in Vaucheria the formation of the wall at the base of the oogonium is delayed until the superfluous nuclei pass back into the parent branch. In the Peronosporaceae the wall is formed when the nuclei are still in the oogonium, thus prohibiting their retreat. The result must be either a multinucleate oosphere or a degeneration of superfluous nuclei. Oltmanns (1895, p. 414) has justly remarked that the condition in Vaucheria is very like that in Fucaceae, presenting only such differences as are necessitated by the presence of cell walls between the oogonium and the parent branch. The remark applies with equal force to the Albuginaceae.

The probability that the ancestors of the Peronosporaceae and Saprolegniaceae had multinucleate oospheres removes these groups from Vaucheria-like forms. If there is any relationship the connection must have been at a time in the ancestry of Vaucheria before the abandonment of the multinucleate condition of its oogonium. As Oltmanns (1895) says, the passage of many nuclei into the rudimentary oogonium in Vaucheria is most readily explicable on the assumption that it once produced many gametes instead of the one that is now habitually found, a view that must meet quite general acceptance, as may be seen from the recent paper of Blackman (1900) and the literature there cited.

Mycologists generally acknowledge the close relationship between the Peronosporaceae, Saprolegniaceae, and Mucorineae. The presence of a multinucleate oosphere and antheridium, and the fusion of two multinucleate masses of protoplasm, quite

naturally suggest a possible derivation of the two former groups through the latter. However, as Schröter (1893) has remarked, "Durch das vollständige Fehlen von Schwarmsporenbildung, das oft rein fädige Mycel, die fast nur an der Luft terminal gebildeten Sporen entfernen sich die M. immer weiter von den Algen;" and it is difficult to regard the Mucorineae ancestral to these other Phycomycetes. The manner in which the Mucorineae may have arisen from ancestral algae has been discussed by Davis (1900, p. 308), who has indicated the similarity between the coenogametes of Mucorineae and those of *A. Bliti*. Notwithstanding this similarity it does not seem advisable to regard the Mucorineae as a line productive of such forms as the Peronosporaceae and Saprolegniaceae for the reasons expressed above. The similarity of the vegetative body, however, is sufficient to indicate the possibility, even probability, that the Siphoneae, Mucorineae, Peronosporaceae, and Saprolegniaceae constitute three distinct lines of development from a common parent stock.

Since transition stages in the evolution of these groups are not known, the phylogeny of the coenogamete is little more than a matter for speculation. Two modes of origin are conceivable; either the coenogamete arose from a gametangium producing numerous gametes through the failure of the gametes to separate and become completely individualized; or it may be regarded as a structure, originally multinucleate, which arose and attained sexual differentiation through a line of ancestry composed of multinucleate zoospores.

According to the first view the coenogamete is morphologically a gametangium or physiologically a compound gamete. Each nucleus is the nucleus of a gamete. According to the latter view the coenogamete itself is homologous with a gamete, being a multinucleate gamete. Arguments in support of either view must be based upon such fragmentary evidence as is afforded by the present existing species (which may be made to stand for stages in phylogeny), or the partial repetition of phylogeny through ontogeny. Unfortunately, very little evidence can be

expected from ontogeny, since the conditions prevailing during oogenesis are such that any vestigial attempt to individualize gametes from the nuclei would be at once obliterated. Naturally the individualization of gametes would without doubt become quickly eliminated from ontogeny after fertilization *en masse* became a fixed habit. Perhaps some one of the other eight species of *Albugo* may exhibit in the oogonium vestigial traces of older conditions and a more perfect individualization of gametes, as the conidia in many *Peronosporineae* develop zoospores which later merge their individuality into a common mass of protoplasm when the conidium germinates by means of a tube. If the multinucleate sex cells were primitively multinucleate, if there has been an independent line of development starting with multinucleate zoospores and leading through multinucleate isogamous gametes to the coenogamete, it might be expected that some structures indicative of such evolution would now be found among living plants. But there are no stages of such a character known, nor is there any group among the algae or fungi which promises to supply them. Possibly the most suggestive group is the *Monoblepharadineae*, which has recently been investigated by Lagerheim (1899), who finds only one nucleus in the rudimentary oogonium, and as many nuclei in the antheridium as there are sperms to be formed. There is much evidence, however, to support the hypothesis that the coenogamete is homologous with many gametes, which have failed to separate. This hypothesis postulates an origin from uninucleate, swarming gametes, generally present in coenocytic algae, as *Hydrodictyon* (Artari 1890), *Dasycladus* (Berthold 1880), *Acetabularia* (DeBary and Strasburger 1877), *Protosiphon* (Klebs 1896), not *Botrydium* (Rostafinski and Woronin 1877) as is so often erroneously cited,¹ thus showing the prevalence of this mode of sexuality among the algae that are usually looked to for the ancestry of the Phycomycetes. The elongation of the sperm nuclei as they lie in the antheridial tube may also be regarded as indicative of an ancestry in which each nucleus was the

¹ For the most recent work on these species see Iwanoff, 1898.

nucleus of an individual gamete. The fact that Phycomycetes, in conidia and oospores, sometimes lose the ability to individualize their units has an important bearing on the problem. It is well known that the contents of conidia and oospores ordinarily separate into as many regions as there are nuclei, and that these develop into zoospores, each unquestionably an individual. However, if these spores, by a change of external conditions, are induced to germinate by means of a tube, the zoospores do not emerge as individuals. Not merely is there a failure to resolve the protoplasm into individuals, but there is an actual surrender of individuality after it has been attained. Not only does this occur in ontogeny, but it is a very generally accepted belief that it likewise occurred in the phylogeny of this group. In the more primitive forms which germinate by zoospores individualization is not abandoned but is merely delayed, since in germination each fusion nucleus or each of its immediate descendants develops its own plasmaderma and begins independent life. In such form the phenomenon is comparable to delayed wall formation in endosperm, with the remarkable exception that in *Albugo* fertilization occurs during the period of delay.

Pyronema (Harper 1900) may be regarded as an excellent illustration of a condition in which the individuality of the sexual nuclei habitually finds expression only through their behavior in the act of fertilization. The manner in which the fusion nuclei wander away immediately after fertilization, and the absence of units in the cytoplasm, are strikingly similar to *Albugo*, as are also the mitoses of the nuclei during oogenesis, the marshaling of the nuclei into a hollow sphere, the participation of the oogonium in the dissolution of the wall adjacent to the antheridium; even the trichogyne resembles in many respects the receptive papilla of *Albugo*.

While certain Ascomycetes resemble the Florideae more than they do the Phycomycetes, the points of similarity mentioned above between the Phycomycetes, *Albugo*, and *Pyronema*, are sufficient to justify careful scrutiny of all features before

abandoning the view held by DeBary (1884) concerning the relationship of these two latter groups. Zoosporangia have not yet been studied cytologically with the completeness they deserve, and it is unwise to deny the possibility of relationship between the ascus and the sporangium until both cell and cilia formation in the Phycomycete zoosporangium is understood.

As the conidia in phylogeny and ontogeny stand for zoosporangia, it is clear that they represent masses of potential zoospores, and are consequently synplasts in the sense in which that word was used by Hanstein (1880). The vegetative coenocyte that develops from the spore is also a synplast, which in phylogeny (and often in ontogeny) goes back to a time when each nucleus governed a definite region of cytoplasm. The multinucleate condition of this vegetative body results from a retardation of cell division, similar to that in the embryo sacs, particularly well illustrated in the gymnosperms, and in the eggs of insects (Hertwig 1892). In the latter forms the delay is not maintained long in ontogeny. Cell division follows soon after nuclear division. In the coenocytic algae there is failure to individualize during a whole generation. Existing forms show that the vegetative body was coenocytic long before the gamete became so. In *Albugo*, the multinucleate condition of the female sexual cell may be regarded as the result of pushing the synplast habit one step further in ontogeny. The sexual cells were the last to give up their individuality, the vegetative cells the first.

The synplast in the Phycomycetes differs from that of most spermatophytes in many ways, most strikingly, however, in the mobility of its potential units. While it is phylogenetically equivalent to many cells, a compound of potential cells, in the sense that Hertwig (1892) uses the expression, the phycomycete synplast, both in sexual and asexual parts, must be regarded as a morphological unit. The potential units have lost their definite limitations and so their morphological value. Discussion regarding the nature of the vegetative coenocyte may be found in numerous texts, as Strasburger (1880, pp. 372, and 1893), Zimmermann (1896, p. 10), Haberlandt (1896, pp. 12-62),

Verworn (1897, pp. 74-78), Pfeffer (1897, pp. 49-51). It is unnecessary to quote these authors or repeat familiar discussion here, further than to state that they agree in general with the statement of Pfeffer (1897, p. 51), "Auch derartige Erwägungen zwingen dazu, zunächst den veilkernigen Protoplasmata als eine morphologische und physiologische Einheit anzusehen."

There is but little in common between the coenogamete, which is a structure of high physiological efficiency, and such structures as have been described by Golenkin (1900) and Klebahn (1899) in *Sphaeroplea*, which, as Klebahn remarks, resemble cases of polyspermy. They seem to indicate a pathological rather than a normal condition.

The strict maintenance of the individuality of the nuclei and their characteristic behavior in fertilization adds another strong argument to the evidence, which is becoming cumulatively great, that these structures are the bearers of hereditary characters. The apparent ease with which one nucleus can usurp the cytoplasm of many is an argument against the energid theory of Sachs.

[*To be concluded.*]

BOTANICAL INSTITUTE, BONN.